

59. *A. vittaticollis* Rand.

"One specimen taken by F. W. Nunenmacher in Josephine County, Oregon, May 8, 1910, and two by myself at Carrville, Trinity County, California, July 1, 1913, on willow." Dr. Van Dyke.

60. *A. walsinghami* Cr.

Type locality, Yreka, California. Others have been taken in same region; also in Inyo County, California. It breeds in one of the desert shrubs.

61. *A. nevadensis* Horn.

Western Nevada type locality. There are in the Van Dyke collection specimens from the Yosemite Valley taken on poplar. It may possibly extend farther north.

Notes on some recent studies of Dragonfly Wing Tracheation (Odon.).

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It was a fortunate day for the progress of our knowledge of the Odonata when R. J. Tillyard began his observations on the dragonflies of Australia. Previously many interesting species had been described from that country, but they were all known merely as museum specimens and known only from bare systematic descriptions drawn mainly by writers in other lands. It is fortunate when the fauna of any land is studied on its own soil; but in the case of Australia it is especially fortunate because of the large number of archaic types there occurring, concerning which a more intimate knowledge has long been desirable.

Such knowledge has been furnished by Tillyard in a large measure; knowledge of life-histories and of habits, of ecology and distribution, of structure and development; and it is being published in a series of fruitful papers of so great value that every Odonatologist must wish that the series may long continue.

Two of these papers¹ deal with wing tracheation, and, like the others, are based on a large first-hand accumulation of facts. Especially valuable is the contribution to the knowledge of the development of the Cordulinae, a subfamily that is represented in Australia by many remarkable forms. But all the groups of the available fauna have been extensively drawn upon.

Tillyard's studies of tracheation extend and entirely corroborate my own² in so far as facts are concerned; but he offers a different interpretation of two matters: (1) the anal veins of the Anisoptera; (2) the radial sector of the Zygoptera. I desire to restate my views concerning these in the light of the new evidence and arguments he has produced.

Tillyard's interpretation of the anal region of the Anisopteran wing differs but little from my own. He found, as I did earlier, that the anal trachea is closely approximated to the cubital for a distance and then descends through an apparent cross vein; then bends again sharply outward and follows thereafter the direct course of the anal vein. He proposes to call the apparent cross vein the "anal crossing," and this I consider an excellent descriptive term and better than "basal cubito-anal cross vein," whether it were originally a cross vein or not; in one instance at least he has shown it is not the most basal of the series of cubital-anal cross veins. Tillyard would call the vein that forms about the conjoined portion of the cubital and anal tracheae Cu+A; and I see no serious objection to this, especially since he then disposes of the vein hitherto known as the anal by a device so little inconvenient as merely labeling it A³. It was not merely the thought

¹Tillyard, R. J. On some problems concerning the development of the wing venation of Odonata. Proc. Linn. Soc. N. S. Wales 39: 163-216, 3 plates, 1914.

Tillyard, R. J. On the development of the wing venation in Zygopteran dragonflies with special reference to the Calopterygidae. Proc. Linn. Soc. N. S. Wales 40: 212-230, 6 text figures, 3 plates, 1915.

²Needham, J. G. A genealogic study of dragonfly wing venation. Proc. U. S. Nat. Mus. 26: 703-764, 14 plates, 44 text figures, 1903.

³In his studies of tracheation of the Chrysopidae (Proc. Linn. Soc. N. S. Wales 41: 221-248, 1916), Tillyard also uses this simple device most opportunely to obviate a cumbersome terminology when apparently simple and direct veins are variously compounded. The condition there pointed out was previously noted by McClendon (Ent. News 17: 120, 1906).

of an encumbered terminology, however, but a doubt as to real homologies of the vein that kept me from doing something like this earlier. I found that the anal trachea originates in the position of the straight adult vein, and only later in development moves up against the cubital, becoming twice angulated. I found the extreme base of the wing saclike and open, its membranes tardily fusing to delimit the vein cavities; and it was easy to conceive that a small marginal trachea, like the anal, occupying a constricted place at the base of the wing might have slipped over where there was obviously more room; and there was and is much doubt in my mind as to whether the vein ever went along with the trachea. This doubt was not resolved by reading Tillyard's paper, for he brings in no new evidence whatever, and I have not his confidence in the constancy of the tracheae. However, Professor Comstock, on reading his paper, set about it and found some new evidence. He reasoned that if the base of the so-called anal vein be a secondary development, some fossil form, if primitive enough, might show its absence. At once he found a single figure of a fossil *Aeschna liassina* of Brodie, which shows this condition. At least the drawing as offered by Brodie⁴ and copied by Handlirsch⁵ shows it. In other parts of the wing, however, this drawing shows obvious inaccuracies. Wherefore, I desired to have the facts confirmed; so I wrote Mr. Herbert Campion to request a re-examination of the specimen. He wrote at once that he thought it was in the Warwick Museum, but on the 13th of May, 1916, he wrote again that it could not be found. Assuming the correctness of this detail of the figure, the best evidence now available seems, therefore, to be in favor of Tillyard's interpretation.

Tillyard's interpretation of the radial sector of the Zygoptera differs utterly and irreconcilably from my own. He found, as I did earlier, that the trachea corresponding to the radial sector is not attached to the radial trachea in any of the Zygoptera, but appears as an added branch of the median tra-

⁴Brodie. Fossil Insects of the secondary rocks of England, Pl. 10, Fig. 4.

⁵Handlirsch. Die fossile Insecten, Pl. 42, Fig. 1.

chea. If this trachea be conceived as a new development from the median stem, I see no particular objection to labeling it Ms; if it be the old original branch from radius that has found a new basal attachment it should still be labeled Rs; but the vein which follows it I cannot believe to be other than Rs of Anisopteran wings. As to the adult vein, I entirely agree with Mr. Campion in the opinion expressed in his letter of March 18th last when he said: "That the Zygoptera do not possess Rs at all is a rather startling proposition and hardly one which can be accepted offhand. In Zygopteran and Anisopteran wings alike we find six longitudinal veins to be all located between R and M. These veins occupy exactly similar positions in the two kinds of wings, and I find it exceedingly difficult to believe that they are to be interpreted in one way in the Zygoptera and in another way in the Anisoptera."

Tillyard demands ontogenetic evidence; and yet, singularly enough, in support of his "unbranched radius theory" he offers just the evidence I lacked to give me the greatest assurance in the other interpretation. This evidence is not from tracheae, however, but from cuticularization of the nymphal wing—a sort of evidence which he himself stresses heavily in support of his theory concerning the development of the anal area of the wing. This cuticularization (anticipatory venation) of the nymphal wing he shows in his text Fig. 5 (Proc. Linn. Soc. N. S. Wales, 40; 227). This shows an actual crossing, for which Dr. Ris' statement that it is "preparatory to the development of the imaginal venation" is no explanation whatever. There is nothing like it in insect wings, except in oblique veins where tracheae either are present or have been present in earlier stages of development. This crossing follows exactly the course taken by the trachea Rs in the more generalized Anisoptera and is probably the channel which that trachea once occupied. It is for me a most satisfactory confirmation of the identity of the vein Rs of the two suborders of Odonata.

Such differences of interpretation grow out of different

ideas as to how the tracheation should be used as an aid to determining the homologies of veins. The tracheation of a nymphal insect wing is never identical with the venation of the adult wing. It may correspond closely; it may entirely diverge. Tracheation affords complete confirmation of vein homologies in some of the lower orders, such as Plecoptera and Corrodentia; it is worthless for such use in other orders, such as Trichoptera and Diptera. It is an aid in most orders, but needs to be used with discretion and with a regard to its limitations. The interpretation of vein homologies by the study of the antecedent tracheae is a method which, like most other methods that we use in zoology, is of value only for what it shows. It is not all-sufficient. Let any one who is inclined to trust to tracheation too far read Miss Morgan's study of Mayfly tracheation⁶ and learn caution.

The Odonata are not alone in furnishing examples of the replacement of one principal tracheal branch by another, independent of adult venation. In explanation of its occurrence in the Zygoptera in my paper of 1903² (p. 713), I cite the parallel well known case of the attachment of trachea M₁ to the radius in *Pieris*, a shift of tracheae which has never led Lepidopterists to change the designation of the adult vein. Indeed Tillyard himself is not consistent; for in the second of the two papers here under consideration he labels and discusses as branches of A, certain tracheae that spring from the cubital stem! If branches of the anal trachea may be shifted without disturbance of the adult vein, why may not those of the radial?

Fortunately, sufficient comparative study will enable one to learn when such shiftings have occurred, so that even in specialized groups the testimony of the tracheae is not wholly invalidated. But if we proceed to change the designation of adult veins without first learning this we shall create for ourselves intolerable and unnecessary confusion.

⁶Morgan, A. H. Homologies of the wing veins of mayflies. Ann. Entom. Soc. Amer. 5 : 89-106, 6 text figures, 5 plates, 1912.